

The University of Chicago

EFFECTS OF SOME ENVIRONMENTAL  
FACTORS ON THE PHOTOPERIODIC  
INDUCTION OF BEET AND DILL

A DISSERTATION SUBMITTED TO THE  
FACULTY OF THE DIVISION OF THE  
BIOLOGICAL SCIENCES IN CANDIDACY FOR  
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1940

By

AUBREY W. NAYLOR

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# EFFECTS OF SOME ENVIRONMENTAL FACTORS ON PHOTOPERIODIC INDUCTION OF BEET AND DILL<sup>1</sup>

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 521

AUBREY W. NAYLOR

(WITH SIX FIGURES)

## Introduction

Among other factors of the environment, temperature and photoperiod are important in influencing the disposition of many plants to differentiate floral primordia. This is particularly true for plants of a biennial habit. A number of investigators (2, 8, 14, 18, 19, 20) agree that the promotive effects of low temperature in initiating seed-stalk development may be subsequently decreased at higher temperatures. Inasmuch as the temperature phases of many photoperiodically sensitive plants may be very short and yet effective in influencing subsequent response to light, as is well illustrated by vernalization experiments, care must be exercised in interpreting results in terms either of light reaction or of reaction to temperature.

If an interpretation is to be made in terms of photoperiodic reaction alone, it is necessary to select plants which do not require a temperature phase in order to render them sensitive to the proper photoperiod for flowering. Since some of the work reported here was performed to determine whether the theories of floral initiation which have been advanced (4, 12, 5) can be used to interpret the flowering response of long-day plants, the plants used were not temperature limited.

Dill (*Anethum graveolens* Linn.) was previously reported (7) to be a sensitive long-day plant having a short induction period and the ability to produce quickly a flowering stalk after four long photoperiods when returned to short photoperiod conditions. MURNEEK (13) has recently emphasized the sensitivity of dill, and in addition has pointed out that it, like Biloxi soybean, will flower if kept for sufficient time on photoperiods not considered conducive to flowering. Previous work had also shown that dill did not require a low temperature treatment in order to be photoperiodically sensitive.

The variety of beet (*Beta vulgaris* L.) chosen differs from most varieties in that it does not have a definite temperature phase. There has been very little modifica-

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tion in its flowering response over rather wide temperature ranges in the greenhouse. Another characteristic of this variety is its capacity to flower vigorously after fourteen or more long photoperiods (19–21 hours of light and 5–3 hours of darkness) when returned to short photoperiod (8 hours of light out of 24).

The dill seeds were obtained from commercial sources; the beet seeds were obtained from Dr. E. Carsner, Riverside, California.

### General methods

No attempt was made to regulate either the temperature or the humidity of the greenhouse, other than to prevent excessively high or low temperatures. The rooms were heated whenever the temperature fell below 18° C. and ventilated when temperatures rose above 32° C. Humidity was partially controlled by spraying the walks and walls with tap water. The plants were watered twice daily with tap water and at intervals with a modified SHIVE'S (16)  $R_2S_5$  nutrient solution.

The seeds were germinated in flats containing a light garden soil. After planting the seeds, the flats were immediately placed either on benches or trucks and subjected to cycles of the desired photoperiod. The beets were usually germinated on shallow greenhouse benches of the usual type, except that they had low rectangular wooden frameworks arranged over them. These frames supported a double thickness of black sateen cloth which was placed over them nightly to control the length of the photoperiod. The dill seeds were germinated on small trucks which were rolled into light-tight sheds each evening.

In the course of the work with dill, it was found necessary to transplant the very young seedlings from flats to  $\frac{3}{2}$ -inch pots. If the leaves had attained a length of 4–5 inches and there were more than three or four expanded leaves present at the time of transplanting they were considered unreliable test plants, since they tended to flower spontaneously even though maintained on cycles of short photoperiod. The cause of this tendency to flower has not been investigated critically, but there is some evidence that injury to leaves and roots during the transplanting process may in some way alter the metabolism of the plant sufficiently to bring about flowering. Further evidence to support this viewpoint is given later. All dill plants were maintained on a 9-hour photoperiod until they were used experimentally.

The beet seedlings were transplanted singly to  $\frac{3}{2}$ -inch pots when their leaves were 4–6 inches long. After transplanting they were returned to the short photoperiod benches. These benches were covered each evening at 4:00 P.M. with the black sateen cloths and were uncovered the following morning at 8:00 A.M., thus affording 16 hours of darkness and 8 hours of light.

The response considered of primary importance in both plants was the change from the rosette condition of the main axis to elongation of the stem or seed stalk.

Elongation of the stem was not always accompanied by production of normal, fertile flowers. In some instances beet stems would be slightly elongated but fail to produce flowers, or if flowers were formed they were reduced in size and sterile. This type of response was usually the result of what was considered incomplete induction. In all the experiments with dill, rapidity of response was measured in terms of the average length of the stems at the time of harvest. Dill plants were usually harvested in any given experiment when the inflorescences of the plants receiving any one treatment began to unfold.

### Investigation

#### EXPERIMENTS WITH DILL

The experiments were planned to test the effects on vegetative growth and reproductive response of (a) continuous illumination of varying intensities from time of germination; (b) continuous illumination of relatively constant intensity from time of germination; (c) interrupting the dark portion of the cycle with light for different lengths of time; (d) high light intensity while on short photoperiod, followed by high intensity on long photoperiod or by low intensity on continuous photoperiod; (e) low light intensity followed by intensities varying from 50 to 1000 foot-candles; (f) different intensities of red light on number of days necessary for induction; (g) low temperature during induction period on flowering response. Another experiment was performed in order to determine the effect of certain types of injury on subsequent development of dill.

CONTINUOUS ILLUMINATION OF VARYING INTENSITIES FROM TIME OF GERMINATION.—To determine whether dill will germinate and grow to maturity under conditions of continuous illumination of high intensity, seeds were germinated in the greenhouse April 18, 1940. These seeds were scattered on the surface of the soil, which was kept moist by frequently sprinkling with a fine spray. Natural daylight was supplied from 8:00 A.M. to 5:00 P.M., at which time a reflector containing six 36" Mazda fluorescent lamps of the daylight type was lowered into position over the seeds. The lamps, affording approximately 750 foot-candles at the soil surface, were used until the following morning at 8:00 A.M., when they were removed.

Germination began approximately 1 week after planting. Instead of the typical rosette type of growth, the stems elongated but grew only slightly in diameter. Approximately 40 days later the plants had attained a height of about 10 cm. and began unfolding their inflorescences. Since the light intensity during the first half of the experiment was more than 700 foot-candles and never fell below 200 foot-candles, it is evident that neither darkness nor light of very low intensity is necessary for the flowering response of dill.

CONSTANT ILLUMINATION AT RELATIVELY CONSTANT INTENSITIES FROM TIME OF GERMINATION.—This experiment was set up in a darkroom where the sole source



of illumination was from Mazda lamps of the daylight fluorescent type. One lot of seeds was planted at the surface of the soil, where light intensity was adjusted to approximately 1000 foot-candles. Another lot was planted similarly except that the light intensity was adjusted to approximately 500 foot-candles. The lamps burned constantly during the experiment. There was, however, a gradual increase in intensity at the surface of some of the leaves as the plants grew, since the reflectors were never readjusted. The highest intensity registered under the first reflector was approximately 1400 foot-candles and under the second, 750 foot-candles.

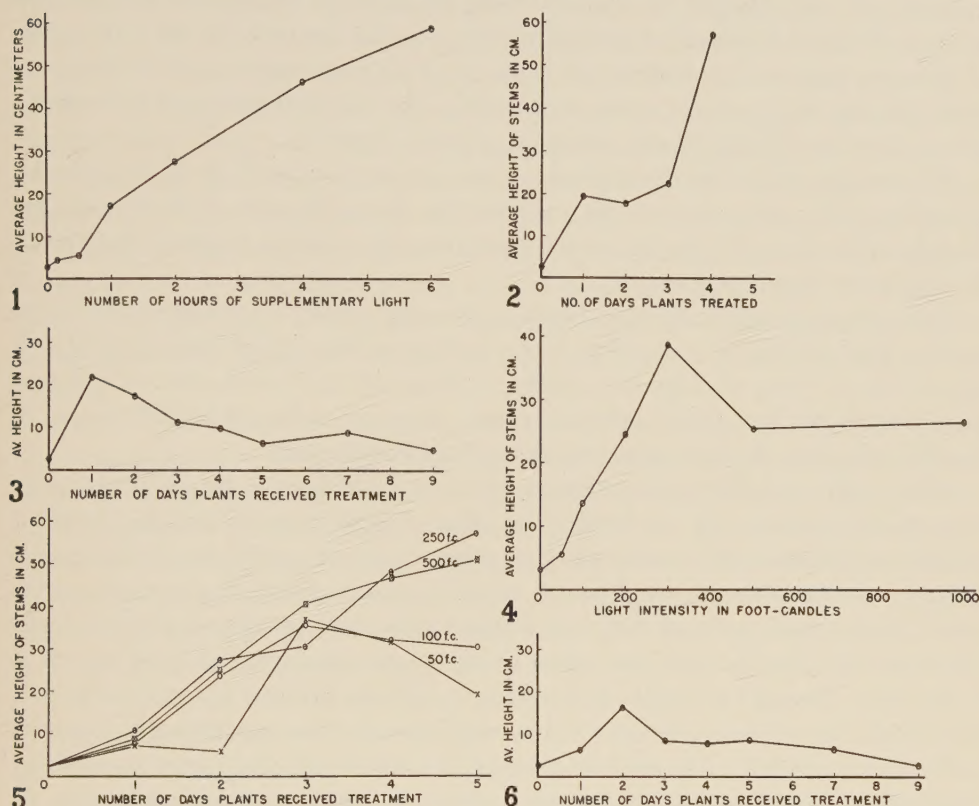
The plants germinated under the highest intensity grew rapidly and were sturdy. For about 30 days they remained as rosettes. After 40 days, stems of a few were elongating. Thereafter many others began to respond. Inflorescences appeared when the plants were 15–20 cm. tall. In contrast, the plants germinated under the lower light intensity grew slowly, were more succulent, and were easily bruised. They remained in the rosette stage for approximately 2 months. Several plants then began to elongate and continued to until the conclusion of the experiment September 10, when sixty-eight plants had elongated to some extent. Some stems attained a length of 50 cm. before inflorescences appeared but were bent over because of weakness.

INTERRUPTING DARK PHASE OF CYCLE WITH LIGHT FOR DIFFERENT LENGTHS OF TIME.—It has been reported that dill requires at least 14 hours of light per day for about 4 days to result in stem elongation. Inasmuch as some short-day plants react as though on long photoperiod when they are given short cycles of light during the dark period (5, 17, 10), tests were made to determine the response when the dark period was interrupted by an interval of light. Three hundred uniform dill plants  $2\frac{1}{2}$  months old were distributed approximately equally in seven small framework compartments. All the plants received daylight 9 hours out of each 24. The plants were then darkened and supplied in six of the compartments with Mazda filament light of approximately 100 foot-candles at the leaf surface, the amount of light being automatically controlled by time clocks. Six different photoperiods were given in the middle of the dark period, ranging from 10 minutes to 6 hours. The plants in one compartment remained in darkness and served as controls. Treatment was continued for 40 days, at which time the plants receiving 6 hours of light as an interruption of the dark period were apparently at their maximum height and were beginning to shed pollen. Measurements of the length of stems of all the experimental plants were then made and averages taken (fig. 1).

Groups of plants having the dark period interrupted for either 10 minutes or 30 minutes elongated no more than the controls. In contrast, those plants receiving 1 hour of supplemental illumination (that is, a total of 10 hours of light out of each 24) elongated several centimeters during the treatment. This point is of particular



interest since the total amount of light during these 10 hours was 4 hours less than is required for stem elongation if the photoperiod is given uninterruptedly. With increasing duration of illumination (fig. 1) during the dark period up to 6 hours, the average height of the plants was almost directly proportional to the amount of supplementary illumination received.



FIGS. 1-6.—Dill: Fig. 1, effect on stem elongation of supplementary light of approximately 80 foot-candles given during middle of dark period (9 hours of daylight each day; measurements taken 40 days later). Fig. 2, response of plants receiving indicated number of cycles, each consisting of 20 hours of light and 4 of darkness (measurements taken 45 days later). Fig. 3, response of plants receiving continuous illumination of 4 foot-candles (measurements taken 45 days later). Fig. 4, effect of continuous light, given after plants had been subjected to 3 short days of low light (measurements taken 51 days later). Fig. 5, effect of red light of various intensities (measurements taken 60 days later). Fig. 6, response of plants receiving cycles, each consisting of 20 hours of light and 4 hours of dark at temperature  $4.5^{\circ}\text{C}$ . (measurements taken 36 days later).

HIGH INTENSITY PREVIOUS TO INDUCTION FOLLOWED BY HIGH INTENSITY DURING INDUCTION.—Under light conditions prevailing in January and February at Chicago, dill has an induction period of 4 days (7). Since light intensity plays an im-

portant role in floral initiation (1, 5), an experiment was performed to determine whether the average higher light intensity of June would appreciably alter the number of days required for induction. On June 15, 1939, fifty-two plants were placed on long photoperiod, while thirteen plants remained on short photoperiod as controls. The long photoperiod, consisting of 20-21 hours of light and 4-3 hours of darkness, was obtained by supplementing the ordinary day length with 80-100 foot-candles from Mazda filament lamps until 2:00 A.M. On each day for 4 days, lots of thirteen plants were transferred from the long photoperiod to conditions of short photoperiod, and the stems measured 44 days after the start of the experiment. Average heights of each group are given in figure 2.

The average height of those plants receiving one, two, and three long photo-inductive cycles was about 20 cm., whereas the average height of those receiving four was approximately 60 cm., about three times the average height of the plants having fewer long photoperiods.

Since plants of which the axes begin to elongate almost invariably flower, it is evident that dill can be induced to flower during periods of high light intensity, if given only one long photoperiod. Speed of elongation and production of inflorescences are much less rapid, and total height attained at the time of flowering is usually less, than in plants receiving four long photoperiods.

HIGH LIGHT INTENSITY PREVIOUS TO INDUCTION FOLLOWED BY LOW INTENSITY DURING INDUCTION.—To test further the effect of light intensity and the duration of light in relation to the rosette and non-rosette types of growth, the following experiment was performed. On June 15, 1939, 104 plants which had been grown on short photoperiod were selected and divided into eight groups of thirteen each. Of these, the plants composing seven groups were transferred at 5:00 P.M. to a room where the light intensity (derived from a Mazda filament source) was 4 foot-candles at the surface of the leaves and was maintained at a practically constant temperature of 26° C. The thirteen plants of the remaining group were maintained on short photoperiod as a control. One group of plants receiving continuous illumination was returned to the short photoperiod trucks each day at 5:00 P.M. for the first 5 days, another group was returned on the seventh day, and the final group was returned on the ninth day. Thirty-eight days after the last transfer was made the plants were harvested and measurements of the flower stalks made (fig. 3).

Plants receiving only 1 day of continuous illumination of low intensity grew most rapidly after being replaced on short photoperiod and attained the greatest height; those treated 2 days grew a little less rapidly; and those treated 3 days grew still more slowly. The groups receiving a greater number of days of treatment differed among themselves so little in average heights that no significance can be attached to treatment longer than four 24-hour periods.



Since light intensity previous to treatment was high, one explanation for the growth effects following the first 24 hours of continuous illumination is that the threshold value for partial induction was reached with the addition of this light, even though it was of low intensity. These plants, of course, received a high light intensity on a short photoperiod 1 day after they had had enough light for induction. If the plants received 72 or more hours of continuous light the effect was apparently negligible. Evidently the light intensity was too low for promotion of the stimulus to flower after the first 24-hour period, and the sooner the plants were returned to short photoperiod where the light intensity was higher the more they responded by elongating. Also, continued exposure to the low light intensity may have depleted the carbohydrate reserve to the point where it was impossible for the plants to recover sufficiently to produce a vigorous flower stalk. If carbohydrate reserve was a limiting factor, it was just as limiting (expressed in terms of subsequent stem elongation) after 4 days of treatment as after 9. In addition it should be noted that, shortly after returning the plants to high intensity in the greenhouse, they recovered their green color rapidly and in most cases appeared normal.

SHORT PHOTOPERIODS OF LOW LIGHT INTENSITY FOLLOWED BY INTENSITIES VARYING FROM 50 TO 1000 FOOT-CANDLES.—Since dill showed practically no further response to continuous light of low intensity after being subjected to three or more 24-hour periods, it was thought possible to remove the effects of previous treatment with high light intensity by subjecting the plants to three short photoperiods of low light intensity (4–12 foot-candles). Accordingly on September 11, 1939, an experiment was started with plants thus treated, to determine the effect of various light intensities, supplied continuously for 4 days, on subsequent development.

The 175 plants were divided into seven equal groups, 25 in each group, and subjected to different intensities of light from Mazda filament lamps, which were placed at one end of a bench in the darkroom. Six groups of plants were arranged at intensities ranging from 50 to 1000 foot-candles. The seventh group was transferred to short photoperiod at the same time for use as a control. All the plants receiving continuous light at the different intensities for four 24-hour periods were returned to short photoperiod. This was done at 5:00 P.M. in order that the plants would receive a dark period immediately following the treatments. Some plants attained their maximum height and unfolded their inflorescences 51 days after the termination of treatment. Measurements were made at that time (fig. 4).

Up to 300 foot-candles, the average height attained was almost directly proportional to the intensity of light received; the average height of the plants receiving 500 and 1000 foot-candles was almost the same as that of the plants receiving 300. There is an apparent inhibitory effect or lack of stimulation of intensities higher than 300 foot-candles on the rate of elongation of the stems.

RED LIGHT AND NUMBER OF DAYS NECESSARY FOR INDUCTION.—Some work (21) has been done on the effect of red light on photoperiodic response when used to supplement natural day length. SCHAPPELLE (15), who worked with narrow ranges of wave lengths of radiant energy in the red portion of the spectrum, demonstrated with a number of species that when red light only is used during the photoinductive cycle, floral initiation will result. In order to determine whether red light of a number of different intensities would prove equally effective in inducing stem elongation in dill, an experiment was set up June 15, 1940.

The primary source of light was provided by Mazda filament lamps screened by using four thicknesses of red cellophane stretched over sheets of glass. These filters had a transmission range below  $580\ \mu$  of 0 per cent and at  $700\ \mu$  of 64 per cent. To eliminate most of the infra-red and minimize the amount of heat reaching the plants, 2-foot square, glass-bottomed trays about 4 inches deep were placed just below the reflectors and above the red filters. Two of these trays were filled with tap water, which flowed through them constantly. Two others, used for low intensities, had their water level maintained by frequent renewals. Four different intensities were used: 500, 250, 100, and 50 foot-candles. Under each of these, groups of twenty plants each were maintained on long photoperiods, each constituting a cycle of 20 hours of light and 4 hours of darkness.

Different groups of plants received one, two, three, four, and five long photoperiods at the various intensities. Treatment began at 5:00 P.M. after the plants had received 9 hours of daylight. At the conclusion of each of the treatments the plants received 20 hours of darkness and were then returned to short photoperiod. Stem development proceeded slowly until measurements were made on September 2 (fig. 5).

The results indicate that the several intensities provided during a long photoperiod are almost equally effective in influencing stem elongation. Intensities of 100, 250, and 500 foot-candles are relatively equally effective when given in two cycles, whereas two long photoperiods consisting of 50 foot-candles of red light given for 20 hours out of each 24 were more effective than a single cycle. All four intensities were about equally effective in initiating stem elongation when the induction treatment lasted 3 days. When the plants were subjected to four long photoperiods, the plants receiving 250 and 500 foot-candles of red light averaged 43–46 cm. high, while those receiving 50 and 100 foot-candles averaged 30–33 cm. high. There appeared to be a rather steady increase in average height of plants receiving 250 and 500 foot-candles of light with increasing number of photoinductive cycles. On the other hand, those plants receiving 50 and 100 foot-candles increased less in average height after they received three photoinductive cycles, the lack of increase being greatest where the intensity was lowest.



LOW TEMPERATURE DURING INDUCTION PERIOD AND FLOWERING RESPONSE.—The temperature at which *Xanthium* plants are maintained during the dark period is an important factor in determining the number of days required for induction to flower (9). Temperature during the photoperiod apparently alters the time required for induction very little. Since dill does not require a dark period for induction, a test was made to determine whether low temperature has any influence on the number of days required for induction.

One hundred and four plants growing on short photoperiod were selected June 15, 1939. These were divided into eight groups of thirteen each. One of these groups was maintained on short photoperiod as a control. The remaining groups were transferred to a room adjusted to 4.5° C. and controlled to within 0.5° C. Light of approximately 1800 foot-candles at the leaf surface was supplied by an Everready carbon arc lamp to give a photoperiod of 20 hours out of 24. After each photoperiod for the first 5 days, and then following the seventh and ninth photoperiods, one group was returned to short photoperiod in the greenhouse. They were maintained there until July 29, when measurements of the heights of stems were made (fig. 6).

The average height of the plants having had 2 days of cold treatment was greatest of any of the groups. Plants having had 3, 4, 5, and 7 days of the cold treatment were only approximately as tall as those receiving one, whereas those receiving nine cycles reacted as did the controls remaining on short photoperiod.

RESULTS FROM INJURY TO STEM.—Initial attempts to show that there was a transmittable flower-promoting substance in dill appeared promising. Further experiments were conducted with the introduction of a greater variety of controls. The data are briefly summarized as follows. One hundred and sixty-five plants were treated March 31 and April 1 in such a way that injury to the stem always resulted. Previous to the experiment, and for its duration, plants were maintained on a 9-hour photoperiod. Fifty-one plants were in flower at the conclusion of the experiment (May 25), the stems of ninety-eight had elongated, while only sixteen remained in the rosette condition. On the other hand, of the eighty-seven control plants one was in flower and the stems of seven had elongated.

The data indicate that injury to the stem results in a strong tendency to flower. Because of this, care must be exercised in transplanting and subsequent handling.

#### EXPERIMENTS WITH ANNUAL BEET

CONTINUOUS ILLUMINATION OF VARYING INTENSITIES FROM TIME OF GERMINATION.—Since dill, as well as a number of other long-day plants, will flower if kept on continuous day, beet was tested to see whether it required a dark period in order to bolt; that is, for the stem to elongate and to flower. Approximately 100 beet fruits were planted April 18, 1940, on the surface of the soil in flats and placed

in the greenhouse. Supplementary illumination was supplied by fluorescent Mazda lamps of the daylight type from 5:00 P.M. to 8:00 A.M., amounting to approximately 700 foot-candles at the surface of the soil. As the plants grew the reflector containing the fluorescent lamps was adjusted at higher levels. The intensity at the surface of the upper leaves, however, never fell below 200 foot-candles.

The seeds germinated rapidly and within 31 days the plants were producing flower stalks. As previously noted, dill which was growing under the same conditions required 10 days longer to produce inflorescences. Another point of contrast was that the leaves of beet grew large and succulent, whereas those of dill were small and expanded only slightly. Also the flower stalks of the beet were much taller than in dill, some of them attaining a height of over 100 cm., while those of dill averaged 10-15 cm.

Since variability of light intensity might be a factor involved in the speed with which beet responded to continuous illumination, an experiment was set up June 26, 1940, in a darkroom where the sole source of illumination was from fluorescent lamps. One set of lamps was adjusted to give 500 foot-candles at the surface of the soil, while the other gave slightly over 1000 at the same level. These lamps burned continuously and were not readjusted, so that as the plants grew in height the intensity at the leaf surface increased; the maximum attained was 1400 foot-candles. Temperature usually fluctuated about 4° C. during the day and ranged from 18° to 29° C. during the experiment.

When the beet fruits were planted, they were almost completely covered with soil and were thoroughly watered. Germination occurred a few days later. Twenty-eight days after the experiment was begun two of the plants receiving the highest intensity were developing inflorescences while the internodes of twenty-four had elongated. After 51 days the experiment under the highest intensity was terminated. By that time seventy-eight plants had bolted. The experiment under the lower light intensity was continued 25 days longer. At that time none of the plants had bolted. All grew vigorously vegetative, however, and had large deep green leaves.

CONTINUOUS ILLUMINATION AND NUMBER OF DAYS REQUIRED FOR INDUCTION.—It has been reported (5) that annual beet will flower if given fifteen or twenty photoperiodic cycles each consisting of 19 hours of light and 5 hours of darkness. To determine the effect of a longer photoperiod on the number of days for induction, 220 uniform plants were divided into two equal groups and transferred from cycles consisting of 8 hours of light and 16 hours of darkness to the following treatments. One group was placed on cycles of 21 hours of light and 3 hours of darkness; the second group was transferred to continuous light. After all the plants had received eight cycles of their respective treatments, ten were transferred each day from each of the two treatments to cycles consisting of 8 hours of light and 16



hours of dark. This was continued until the last group of plants had received eighteen cycles. Approximately a month later it was found that half the plants which had received continuous illumination for 11 days had bolted. Slightly more than half the plants receiving twelve cycles, each consisting of 21 hours of light and 3 hours of dark, had bolted. The internodes of such plants were relatively short and the leaves on the stems were larger than those on the plants which received thirteen or more cycles of either continuous light or 21 hours of light and 3 hours of dark. From their appearance the stalks seemed to be more leafy than completely induced plants. Bolting in plants having received 11 days of continuous light was little more pronounced as to height attained and was only a little more rapid than in plants which received the other treatment. The data indicate that thirteen or more cycles conducive to flowering are necessary before annual beet will be as completely induced, as shown by its bolting characteristics, as plants maintained continuously on cycles consisting of 21 hours of light and 3 hours of darkness.

**INTENSITY OF LIGHT REQUIRED FOR INDUCTION.**—In the open greenhouse, where beet was found to be induced on continuous photoperiod and on cycles consisting of 21 hours of light and 3 hours of darkness, the light intensities varied constantly during the day from 6000 foot-candles to approximately 100, and the intensity of supplementary illumination in the various experiments ranged from 70 to 750 foot-candles. There was also considerable diurnal fluctuation in temperature. Because of these variations in light and temperature, an experiment was designed to determine the minimum constant intensity of light which would induce flowering. Early in June forty-five uniform plants were selected from the short photoperiod bench, divided into three lots, and transferred to a basement room where they could be illuminated only by fluorescent lamps. Three arrangements were made, two provided 900 foot-candles at the leaf surface, the other 700. One of the former was regulated to provide cycles consisting of 20 hours of light and 4 hours of darkness, the other burned continuously. The one at 700 foot-candles also burned continuously. Temperatures ranged from 18° to 29° C. during the experiment.

Ninety-one days after the experiment began eleven of the plants receiving continuous light of 900 foot-candles had begun to flower or had elongated. Those exposed to cycles of 20 hours of light and 4 hours of dark responded more slowly, but nine of the fifteen did flower. Of the plants receiving 700 foot-candles continuously all but three remained vegetative. In another experiment, fifteen plants were maintained under conditions of continuous light at 700 foot-candles for more than 3 months, during which time but two plants flowered.

The minimum intensity of continuous light required for flowering in beet is approximately 700 foot-candles. If the intensity were to fall much lower the plants would probably all remain vegetative. Even at 700 foot-candles the plants re-

mained green for the duration of the experiment and appeared to be not greatly different from those grown in the greenhouse continuously. Some time after the plants were placed under the fluorescent lights, however, the newly forming leaves were a darker green than those grown in natural daylight and the plant had two or three fewer leaves, but the leaves were manufacturing sufficient food materials to store starch in the base of the expanded portion.

**CRITICAL DAY LENGTH.**—To determine the critical day length of annual beet, groups of fifteen plants were placed in small dark chambers (April 15, 1940) lighted by Mazda filament lamps providing 80-100 foot-candles at the leaf surface. The photoperiod consisted of 9 hours of natural daylight, supplemented as required to provide 9, 10, 11, 12, 13, 14, and 16-hour photoperiods out of each 24 hours. Two other groups of plants were used as controls. One of these was placed on long photoperiod of about 21 hours while the other received continuous illumination.

Within 20 days all the plants having continuous illumination and those receiving cycles of 21 hours of light and 3 hours of darkness were flowering. Twenty-four days later (June 12) four plants receiving cycles of 16 hours of light and 8 hours of darkness were bolting. By July 21 the remaining eleven plants had flowered or were showing some elongation. On this date four of the fifteen plants receiving cycles of 14 hours of light and 10 hours of darkness were flowering or were elongating. There was no flowering in any of the other treatments. The data indicate that the critical day length for this variety of beet lies between 13 and 14 hours; that is, it does not flower if subjected to more than 9 or 10 hours of darkness in each 24-hour period.

Light intensity is probably an important factor in determining critical day length and in influencing the time necessary for response. On July 9, when the day length was 14 hours and 54 minutes, 120 plants were divided equally into four groups. One group received 21 hours and 37 minutes of light per day, a second 20 hours and 37 minutes, a third 19 hours and 37 minutes, and a fourth natural day length. Illumination supplemental to natural day length was provided by Mazda filament lamps. Owing to the decreasing duration of light per day, the total amount of light received at the end of the experiment was considerably less than at the beginning. Only 17 days later the plants in all three groups receiving supplementary illumination were bolting. Eleven days later nineteen out of thirty of the plants receiving natural day length were bolting.

The indication from a comparison of the speed with which beet responded to natural day length and to 9 hours of sunlight plus 7 hours of Mazda filament light is that either intensity or quality of light given after 9 hours of daylight is important in governing the rapidity with which bolting is induced.



"CUMULATIVE EFFECTS" OF EXPOSURE TO LIGHT.—There has been abundant evidence on the cumulative effect of photoperiodically inductive cycles on subsequent response to both long and short-day plants. This point is well illustrated by those plants which require more than one photoperiod of a definite length for induction. In some plants the requisite number of photoperiodic cycles for induction must be given without interruption. Biloxi soybean is one of these. Under ordinary circumstances it flowers only after exposure to four consecutive cycles consisting of 13 hours of light and 11 hours of dark. LONG (9) demonstrated the presence of cumulative effects, which endured for 24 hours, in *Xanthium*. Evidence from experiments with beet, however, indicates that the effects of ten consecutive cycles consisting of 18–20 hours of light and 6–4 hours of dark may last as long as 16 days, at which time four or five more long photoperiods consisting of 18–20 hours of light out of 24 result in flowering (5).

In order further to examine the tendency of beet to show this so-called cumulative effect of long photoperiods, a number of experiments were performed. Some of these involved the use of cycles of light and dark of equal duration, giving a total of 12 hours of light and 12 hours of dark. GARNER and ALLARD (3) found that if long-day plants were given cycles of light and dark ranging from 6 hours' light and 6 hours' dark to 1 minute light and 1 minute dark, they would respond as though on long photoperiod even though the total amount of light received was less than required for flowering if given continuously.

The outline of procedure was as follows: (a) 5 minutes of light and 5 minutes of dark; (b) 30 minutes of light and 30 minutes of dark; (c) 24 hours of light and 24 hours of dark. Other experiments involved cycles in which the light and dark periods were not of equal duration. One of these was designed to give one cycle with 8 hours of light and 16 hours of dark, followed by one cycle with 21 hours of light and 3 hours of dark; and then each cycle was repeated in order. Another similar experiment was performed in which three cycles, each consisting of 8 hours of light and 16 hours of dark, were followed by three cycles each consisting of 21 hours of light and 3 hours of dark. Flowering occurred in none of these experiments, even though the minimum duration of such continuous treatment in any instance was 2 months.

It has been reported that at least one long-day plant, dill, can be induced to flower by exposing a single leaf to conditions of long photoperiod (7). Repeated attempts have been made to cause beet to bolt by exposing a single leaf to conditions of long photoperiod, but in no instance has this resulted.

A number of experiments with short-day plants have shown that the physiological conditions involved in induction can be transmitted from one plant to another of the same species (6, 11, 12). In some of MELCHERS' work (12) involving the grafting of different species, a vegetative plant was induced to flower when it was

grafted to a different species which was flowering. If other vegetative plants could be thus induced to flower, considerable affirmative evidence could be brought to bear on the hormone theory of floral initiation.

Numerous grafts between different varieties and species were made. Among the grafts tried was one in which annual beet, of an unnamed variety closely related to biennial beet, was approach grafted, in the region of the hypocotyl, to biennial beet. Immediately after grafting the two varieties, they were placed on the long-day bench. After 3 weeks the annual beets were flowering vigorously. Although the grafts took firmly, the biennial beets remained vegetative throughout a period of 2 months, when the experiment was discontinued. All evidence from the grafting experiments indicated that if there was a flower-inducing substance transferred from one plant to another, the biennial variety still did not flower.

### Discussion

With an increase of critical data on floral initiation and vernalization processes, sufficient information is now available to permit some speculation as to the phases involved. Three of the more direct hypotheses which have arisen as a result of vernalization and photoperiodic work have been those of GREGORY and PURVIS (4), MELCHERS (12), and HAMNER (5).

It is significant that while these workers have advanced their theories independently and have used different lines of approach, their conclusions are fundamentally similar. They all agree that there is some substance or physiological condition necessary before photoperiod becomes an active agent in altering the plant's physiology sufficiently to induce it to change from the vegetative to the reproductive state. They also agree that photoperiodic cycles of light and dark can then determine the production of another substance or alter the physiological condition sufficiently to bring about the initiation of floral primordia.

HAMNER (5) has conducted a number of experiments bearing on the subject of floral initiation in two short-day plants, cocklebur and Biloxi soybean. While he is conservative in his interpretations of the substances or conditions involved, he demonstrated that conditions previous to photoperiodic induction could limit, to a certain extent, various activities which occurred during induction. Of course, this might be interpreted in terms of MELCHERS' hypothesis to indicate that the degree or amount of vernalin present had been affected previous to the photoperiodic inductive treatment.

HAMNER was chiefly concerned in his interpretation of the causes related to floral initiation and with the importance of not only the light and dark phases of photoperiodic cycles leading to induction but also of the conditions which prevailed subsequent to the imposition of such cycles or series of cycles. From his work and that of his coworkers, he suggested that there was a physiological condi-



tion or change brought about during the light period which he designated as A; others which took place in darkness were designated as B; and those which might be considered as post inductive were termed C. For brevity of reference he used the progression A, B→C to indicate the entire interrelationship.

In previous experiments involving reactions to 14 hours of light followed by 10 hours of darkness, dill remained in the rosette condition. In these experiments it was found that if the cycle was 9 hours of light and 7 hours of dark, then 1 hour of light and 7 hours of dark, the plants responded by elongating their stems. If more than 1 hour of light was given in the middle of the dark period the stems elongated at a rate almost proportional to the duration of the interposed light phase. This suggests that there is a tendency for dill to assume a physiological condition which becomes increasingly strong for the promotion of stem elongation during the photoperiod, but that during a dark period longer than the critical there is a retrogression to the condition prevailing previous to illumination. This retrogression may be slow and require the full dark period. Light may arrest it. If the dark period is interrupted, therefore, retrogression in this physiological tendency is greatly lessened and the degree to which it is halted is roughly proportional to the duration of light received during the dark period.

That there is a tendency for accumulation of small amounts of some kind of flower-forming stimulus in dill, even though it is on cycles consisting of 9 hours of light and 15 hours of dark, is indicated by the fact that after approximately 9 months of such cycles all of a group of fifty plants flowered within approximately 1 week. The tendency for darkness, in excess of the critical, to retard development of dill as well as other long-day plants may be of varying effectiveness. MURNEEK (13) points out that *Rudbeckia* may be maintained in a rosette condition on photoperiods of 12 hours or less for more than a year, provided the temperature does not become extreme. High temperature, however, will overcome the retarding effect of darkness, and this plant will then react—so far as reproductive response is concerned—as an indeterminate.

In an experiment designed to determine the critical day length of annual beet, further evidence was given for the accumulation of a flower-promoting stimulus. On continuous day beet began to show some stem elongation about 14–16 days after treatment began. Those plants receiving a 21-hour photoperiod began to bolt a few days later. It was not until 12 weeks after the experiment had begun that all the plants having cycles, each consisting of 16 hours of light and 8 hours of darkness, had bolted. After the same interval of time four of the fifteen plants receiving cycles of 14 hours of light and 10 hours of dark had bolted. While this experiment is not conclusive, it appears that over a period of time there is a slow accumulation of the residual effects of light which is slightly in excess of the

critical day length, ultimately reaching a threshold value which results in stem elongation and floral initiation.

Intensity of light was shown to play an important role in altering the physiological state of both dill and beet sufficiently to bring about flowering. In an experiment with dill it was found that when different groups of plants were exposed to different intensities of continuous light, their response in stem elongation was almost proportional, up to 300 foot-candles, to the amount of light received. With beet the plants flowered only after receiving light of 900 foot-candles for 6 weeks. Plants similarly treated, except that the light intensity was 700 foot-candles, flowered in only two cases out of fifteen.

Another environmental factor of importance in altering the response of dill to long photoperiod was temperature. If plants having cycles each consisting of 20 hours of light and 4 hours of darkness were maintained at a temperature of  $4.5^{\circ}\text{C}$ . they were only slightly responsive. The longer they received this treatment the less response they gave. From a theoretical viewpoint this would seem to indicate that higher temperatures are necessary for the efficient change of physiological conditions sufficiently to bring about stem elongation and flowering.

In general it appears that in dill—even under conditions of long photoperiod or in some instances continuous light—the greater the duration (at least beyond 1, 2, and 3 days) of such conditions as exposure to 4 foot-candles of Mazda filament light, temperatures of  $4.5^{\circ}\text{C}$ ., and intensities of red light of 50 foot-candles, the weaker the response in terms of average elongation of stems.

### Summary

1. If maintained on continuous light in the greenhouse, dill flowered in 40 days after sowing the seeds and beet in 31 days. Under conditions of relatively constant illumination at 1000–1400 foot-candles, dill required 40 days from time of planting to show some stem elongation; approximately 20 more days were required to bring about the same response under 500 foot-candles. Under similar conditions of constant illumination of high intensity, beet produced seed stalks 28 days after planting. On the other hand, beet grown under 500 foot-candles did not produce seed stalks.

2. With increasing amounts of illumination during the middle of the dark period, up to 6 hours, the average height of the dill plants was almost directly proportional to the amount of supplementary illumination received.

3. Under conditions of high light intensity, dill may be induced to flower by giving it one long photoperiod consisting of 20–21 hours of light and 4–3 hours of dark. Rapidity of stem elongation was about the same when the plants received one, two, or three long photoperiods. But if the plants received four long photoperiods, they elongated about as rapidly as those maintained on long day.

4. Dill plants previously treated with a high light intensity showed a response to continuous illumination of only 5 foot-candles if exposed to it for as little as 1 day. Those subjected to this treatment for 2 days showed some response, while those having 3–8 days of low light continuously were very slow in responding.

5. When dill was pre-treated with three short photoperiods each consisting of 9 hours of light of 4–12 foot-candles and 15 hours of darkness, and then subjected to intensities of 50–1000 foot-candles, there was a steady increase in average height with increase in intensity up to 300 foot-candles. The effect of higher intensities (500–1000 foot-candles) on rate of stem elongation was approximately the same as that produced by 200 foot-candles.

6. The effect of low temperature ( $4.5^{\circ}\text{C.}$ ) on dill plants receiving cycles consisting of 20 hours of light and 4 hours of darkness was to suppress markedly the flowering response. Those plants receiving 2 days of cold treatment attained a greater height than did any of those receiving fewer or more days of such treatment.

7. A large proportion of young dill plants elongated their stems if the roots or stems were injured. Thus injury seemingly altered the metabolism sufficiently to bring about the flowering response.

8. Red light of wave lengths greater than  $580\ \mu$  are capable of inducing the flowering response in dill when used as the sole source of illumination during the induction period.

9. Although red light of 50 foot-candles was approximately as effective in bringing about induction in dill as any intensity up to 500 foot-candles, it was not nearly so effective after 5 days of treatment as the higher intensities.

10. Annual beet did not flower if it received more than 10–11 hours of darkness in each 24.

11. Annual beet began to bolt after return to short day if it received 11 days of continuous light. The bolting of such plants, however, was no more rapid or pronounced than in those receiving cycles consisting of 21 hours of light and 3 hours of darkness.

12. Continuous illumination with 900–1000 foot-candles of light from white fluorescent Mazda lamps, under conditions of only slight temperature fluctuation, was conducive to flowering in beet. If the intensity did not rise above 700 foot-candles during the induction period, flowering did not occur.

13. Annual beet did not flower if subjected to the following cycles of light and dark: (a) 5 minutes of light and 5 minutes of dark (55 days); (b) 30 minutes of light and 30 minutes of dark (55 days); (c) 24 hours of light and 24 hours of dark (117 days); (d) one short photoperiod of 8 hours of light, 16 hours dark and one long photoperiod of 21 hours of light, 3 hours dark (117 days); (e) three short



photoperiods of 8 hours of light, 16 hours dark and three long photoperiods of 21 hours of light, 3 hours dark (117 days).

14. Exposure of a single leaf of beet to cycles of 20 hours of light and 4 hours of darkness did not result in the plant flowering.

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